Environmental Factors Influencing Reproduction in a Temperate Marine Reef Goby, *Rhinogobiops nicholsii*, and Associated Behaviors

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Abstract.—The blackeye goby is a protogynous reef fish common to the northeastern Pacific Ocean. While this ubiquitous species has been the focus of numerous studies, there are several aspects of its reproductive ecology that are unknown. By directly quantifying reproduction from digital photographs of blackeye goby nests in the field, this study aimed to determine whether reproductive patterns were linked to 1) lunar phase or 2) ambient water temperature; and 3) whether the behavior of gobies changed when a nearby conspecific had eggs in his nest. At Santa Catalina Island, California, twenty 2.25-m^2 artificial reefs were established and stocked with similar numbers and size-distributions of blackeye gobies during the summers of 2012 and 2013. Photographs of nests were taken weekly for ~3 months each summer. Through analysis of photographs, incubation time was found to be more than 7 days but less than 14 days. Nests, each guarded by one male, contained an average of 8664 eggs, in an area of 43.8 cm^2, with 215 eggs cm^{-2}. Blackeye gobies laid eggs during all lunar phases and the number of eggs produced was not related to lunar phase. Reproductive output, however, was negatively correlated with water temperature, with populations on reefs that experienced cooler temperatures producing more eggs. The presence of eggs in a nest had little effect on behavior of blackeye gobies on that reef. Additional observations made outside of summer months indicated that blackeye gobies can reproduce year-round in southern California. These results suggest a reproductive strategy aimed at maximizing total reproductive output by spreading the risk of reproductive failure throughout the year rather than optimizing the timing of reproduction.

In marine animals with pelagic larvae, factors that affect recruitment of settlers into populations are typically better understood than factors that affect reproductive output. This is because it is generally easier to observe recruits than it is to observe reproduction. Thus, much of what we know about reproductive patterns of marine animals is inferred from temporal patterns of recruitment, rather than direct observations of reproduction. For example, reproductive patterns of fishes with pelagic larval phases are often reconstructed from recruitment surveys combined with otolith-based aging. This approach, however, can mask the actual patterns of reproductive output due to high and variable mortality rates during the larval phase (Carr and Syms 2006; Johnson 2008).

As an example, lunar patterns in recruitment could be driven by reproductive timing or by differences in larval delivery or survival that have a lunar basis. Synchronizing larval release with a particular lunar phase that exposes larvae to favorable environmental conditions may provide fitness benefits and has been observed in a wide array of marine taxa (Middaugh 1981; Robertson et al. 1990; Levitan et al. 2004; Fox 2013). Pelagic larvae are thought to be more conspicuous to visual predators during full moons when lunar radiance is greatest (Hobson et al.

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1981); however, photopositive larvae may swim toward the surface during full moons, avoiding predator filled reefs (Thresher 1984). Additionally, internal waves, associated with changes in tidal amplitude driven by lunar phase are thought to influence the probability and timing of larval exposure to suitable habitat and levels of intraspecific competition (Kingsford and Choat 1986; Shanks 1986; Levinton 2009).

Another factor known to affect reproduction of marine fishes is temperature (Abbott 1969; Smyder and Martin 2002; Sims et al. 2004). Generally, embryo and larval development is faster in warmer waters (Pauly and Pullin 1988; McCormick and Molony 1995), reducing incubation time (Ryland and Nichols 1975), and pelagic larval duration (O'Connor et al. 2007). Reproducing during periods of warm water can improve larval survivorship by increasing larval growth rates shifting prey out of size ranges that predators are capable of consuming (the "growth-mortality" hypothesis; Anderson 1988). Conversely, nutrient availability is often inversely related to water temperature (Dayton et al. 1998) and therefore larval growth may increase when water temperature is low and food (e.g., zooplankton) is abundant.

Alongside abiotic factors, behavior often plays a significant role in reproductive success. In fishes, demersal eggs are typically defended by the male and less often by the female or both parents (DeMartini and Sikkel 2006). Behavioral changes, such as increased aggression (i.e., nest defense) and nest maintenance, improve hatching success; however, they may occur at the cost of foraging, predatory avoidance, or further courtship. Population density (Warner and Hoffman 1980) and reproductive territoriality (Hoffman 1983) may further modify behavioral trade-offs. Thus, while altered behavior of a nesting male may improve egg survivorship, it may detract from future mating opportunities by allowing increased courtship and foraging by competing subordinate individuals.

The majority of protogynous (female-to-male sex-change) species, including the study species, exhibit a size-based social dominance hierarchy whereby dominant individuals influence the behavior of subordinate individuals (Cole 1984; Ross 1990). Specifically, alpha males dominate and socially repress growth of nearby individuals, through increased energetic expenditure and decreased foraging rates of subordinates, to maximize their competitive edge and reproductive opportunities (Helfman et al. 2009; Munday et al. 2009). Altered behavior of the alpha male, such as increased nesting behaviors at the cost of intraspecific aggression, could reduce social repression of subordinate individuals.

The blackeye goby (*Rhinogobiops nicholsii*) is a protogynous fish that occurs from British Columbia, Canada to central Baja California, Mexico where it is closely associated with rocky reef habitat (Love 2011). It is common in the waters of southern California. The ubiquity and small size of this species has resulted in its widespread use as a model study species to address ecological questions (e.g. Breitburg 1987; Steele 1996; Yong and Grober 2013). While an extensive body of literature has been compiled on this species over the past 50 years, (e.g. Ebert and Turner 1962; Wiley 1973; Cole 1983), several aspects of the reproductive ecology of this species are still unknown. Ebert and Turner (1962) briefly described blackeye goby reproduction; Wiley (1973) documented food and nesting habits, morphometrics, population structure, and social behavior; Cole (1983) determined that this species exhibits protogynous hermaphroditism; and Breitburg (1987) showed that male reproductive success was limited by the availability of suitable nest sites.

Male blackeye gobies compete for territory that encompasses the territories of multiple females (Cole 1984) through a number of behavioral displays (Wiley 1973). Because blackeye gobies exhibit a size-based social dominance hierarchy, larger males tend to have greater success at acquiring and defending territories that provide opportunities to mate with nearby females (Cole 1983). Male blackeye gobies establish and defend a nest within their territory by digging a

burrow in sand under overhead rock (Ebert and Turner 1962; Wiley 1973). Females lay adhesive eggs on the rock ceiling of the burrow and the male defends and maintains the brood of eggs until they hatch (Ebert and Turner 1962). Larvae are planktonic for 40-76 days before settling to suitable reef habitat (Block 2011).

It is not known, however, whether the reproductive patterns of blackeye gobies change in response to environmental or social stimuli. We directly measured reproductive output by employing artificial nests, an approach used in studies on other small, reef-dwelling fishes (e.g. Knapp et al. 1995; Samhouri 2009; Forrester et al. 2010). We aimed to (1) determine whether blackeye gobies time reproduction with lunar phase, (2) investigate links between reproductive output and temperature, and (3) determine whether the presence of eggs in a nest influences the behavior of nearby conspecifics.

Materials and Methods

General Methods

To evaluate factors influencing reproduction in blackeye gobies, experimental populations were established on twenty rock-rubble reefs in Big Fisherman Cove, Santa Catalina Island, USA (33°26′42″N, 118°29′8″W) during the summers of 2012 and 2013 (Fig. 1A). Each reef was 2.25 m^2 and constructed of ~60 L of rock placed on a PVC frame lined with plastic mesh to keep the rocks from sinking into the sand. Reefs were built on a sand plane at 10–13 m depth, and were 10 m from any other reef structure to minimize movement of fish among reefs. To minimize mortality, each reef was covered with a predator exclusion cage (3.4 and 3.8-cm plastic mesh in 2012 and 2013, respectively). To investigate the influence of temperature on reproduction, six iButton temperature loggers were deployed throughout the reef array in 2013. These recorded bottom temperatures hourly from July 19 to September 13, 2013.

Each reef was stocked with a similar number, size distribution, and sex ratio of blackeye gobies as determined from surveys on natural reefs (Cole 1984, Love 2011, pers. obs.). Densities were 16 ± 4 individuals per 2.25-m^2 reef comprised of 5 ± 2 males, 7 ± 2 females and 4 ± 2 juveniles (mean ± SD, $n = 20$). Gobies were collected with dip nets by SCUBA divers on natural reefs between Lion's Head Point (33°27′08″N, 118°30′05″W) and Little Geiger Cove (33°27′32″N, 118°30′59″W). Sex was determined from genital papillae, an accurate indicator of functional sex and maturity in gobiids (Cole 1983, Cole and Robertson 1988).

Reproductive Output

Reproductive output was quantified via photographs of eggs in artificial nests, using methods similar to those of Forrester et al. (2010) who studied a similar species of goby. Inverted terracotta potting saucers were used as artificial nest sites. A small opening was cut along one edge of each saucer (Fig. 2A), which provided easy access for males and promoted their use over natural rocks. Three saucers were placed on each reef (Fig. 1B). During summer months (July-September), saucers were checked weekly for the presence of broods of eggs, and all broods were digitally photographed. Additionally, from October 2013 to late March 2014, nests were checked and photographed monthly to determine if reproduction was occurring during autumn, winter, or spring.

The digital images were analyzed in Image J (Abràmoff et al. 2004) to estimate the number of eggs in each brood. Images were set to scale, total brood area was measured, and egg counts were made in five 1-cm^2 subsamples. Egg density appeared to be uniform, and therefore the total number of eggs in each brood was estimated as the product of the average density of eggs in the five subsamples and total brood area.
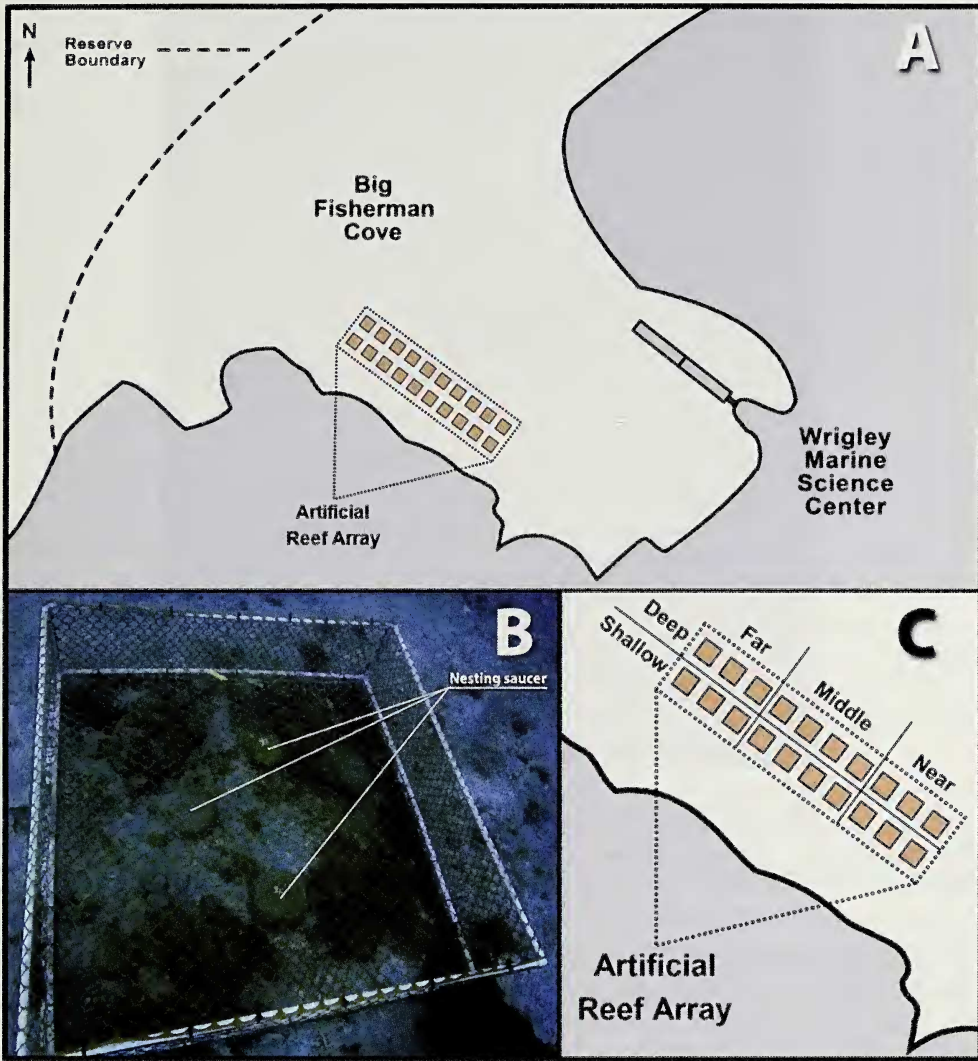
Fig. 1. Artificial reef design. A) Reefs were constructed along the southern side of Big Fisherman Cove in two parallel lines. B) Each artificial reef was composed of four interconnected sub-reefs positioned evenly within the 2.25-m² plot to maximize habitable space. Three inverted terracotta potting saucers served as artificial nests on each reef. C) Reefs were categorized by depth, shallow (~10 m) or deep (~13 m), and position relative to the back of the cove.

Behavior

Behavioral observations were conducted weekly for 7 weeks beginning on July 8, 2012 to determine if behaviors changed when broods of eggs were present on reefs. The behaviors of three classes of blackeye goby, males, females, and juveniles, were recorded. Two divers visited each reef for 6 minutes and each diver observed three fish, one in each class. The first minute of each observation period was spent identifying focal individuals and allowed fish to acclimate to diver presence, and the remaining 5 minutes were spent observing the behaviors of all three individuals. Due to the sedentary nature of the study species, it was not difficult for each diver to independently monitor three fish simultaneously. Large males were targeted
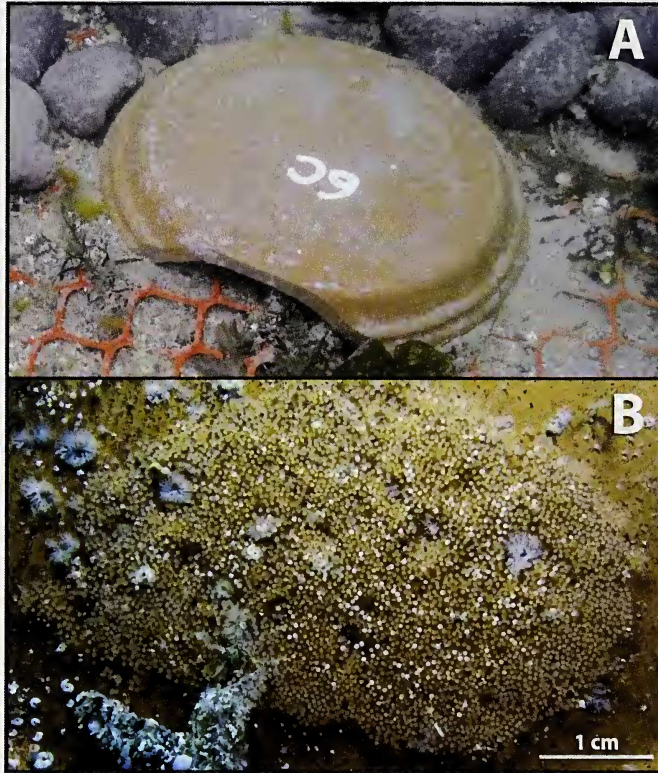
Fig. 2.   Terracotta saucers were used as artificial nest sites. A) A small slot cut along one edge provided easy access for males, promoting use of artificial nests over natural rock. B) Close-up photo of a single brood of eggs on the underside of nesting saucer. Individual eggs are easily identifiable. The scattered eggs that appear white are dead, likely because they were not fertilized or succumbed to microbial infection.

because of their social dominance and influence on conspecific behavior. They were easily identified by their size [>7.5 cm standard length (SL)], black pelvic disc, and close proximity to a nesting saucer. Females were smaller (4.0–7.5 cm SL) and lacked the obvious black on their pelvic disc. Juveniles were smaller than adults (<4.0 cm SL) and were often found at reef margins, likely displaced from optimal reef habitat by territorial adults. The frequency of four focal behaviors defined by Wiley (1973; Table 1), were recorded: aggression, courtship, nesting, and foraging. Divers were unable to communicate to each other which fish they had chosen to

Table 1.   Behaviors recorded, as described by Wiley (1973).

Behavior	Description
Aggression	Flaring fins and/or gaping mouth
	Chasing
Courtship	Flaring fins while undulating body outside nest opening
	Quick rushes in and out of nest
Nesting	Removing sediment or growth from inside nest
	Body undulations within nest entrance aerating eggs
Foraging	Short bursts into the water column picking at particles
	Sifting mouthfuls of sediment for infaunal organisms

observe, therefore, to avoid pseudoreplication, the average of the two divers' observations of each class were used for statistical analyses.

Temperature

Six temperature loggers (iButton thermocron, model DS1921G) were placed throughout the array of reefs to explore potential effects of temperature on reproductive output during 2013. The loggers recorded temperature every hour for nearly two months (July 19 – September 13, 2013). The iButtons were waterproofed inside a pair of male and female end caps (3/4 inch schedule 40 PVC) with Teflon thread tape and included a small dehydration packet to absorb moisture. Temperature loggers were placed in 6 evenly spaced positions relative to the back of the cove (near, middle, and far) and at different depths (shallow or deep; Fig. 1C).

Statistical Analyses

To test for any lunar pattern in blackeye goby reproduction, we used two-way, mixed-model permutational analysis of variance (PERMANOVA) to compare weekly reproductive output among the four lunar stages (new, 1st quarter, full, and 3rd quarter) over two full lunar cycles during July and August, 2012 using reefs as replicates, which were sampled repeatedly. The factors in the model were lunar stage (fixed) and reef (random). Univariate PERMANOVA was used rather than parametric ANOVA because the data were badly non-normal due to a preponderance of zeros (almost half of the observations). An a priori comparison of spring (full and new moons) and neap (first and last quarter moons) tides was conducted to test for any influence of tidal amplitude. PRIMER v6 with the PERMANOVA + add on was used for all permutational analyses.

We had too few temperature loggers to test whether reproduction on each reef was related to temperature on it, so instead, we tested whether reproductive output at reefs in the vicinity of each of 6 temperature loggers ($n = 3$-4 reefs) was correlated with differences in temperature among the 6 positions. Two-way ANOVA was used to test for (1) differences in daily bottom temperature and (2) average reproductive output per week between depths and among positions. Assumptions of normality and homogeneity of variances were met for mean daily temperature and reproductive output after square-root transformation. We tested for a correlation between reproductive output and water temperature in the 6 portions of the study area using a Spearman rank correlation, because the relationship appeared to be nonlinear. SYSTAT 13 was used for these analyses.

We tested whether blackeye goby behavior differed when a brood of eggs was present on a reef. Egg presence was based on nest photos taken 2-3 days prior to the behavioral observations. Permutational multivariate analysis of variance (PERMANOVA) was used to test for differences in behavior, with egg presence in a nest and fish class (male, female, or juvenile) as the two predictor variables and the rates of aggression, courtship, nesting, and foraging behaviors as the multivariate response variables. Rates of behaviors were normalized (mean subtracted and divided by the standard deviation) before constructing a dissimilarity matrix with them using Euclidean distances. PERMANOVA was used rather than MANOVA because the data failed to meet the assumptions of normality.

Results

Reproduction occurred in all months that populations of blackeye gobies were on the reefs, from July to March, with eggs clearly visible within saucer nests (Fig. 2B). Broods contained an average of 8664 (± 349) eggs, in an area of 43.8 (± 1.9) cm^2, with an average density of 215
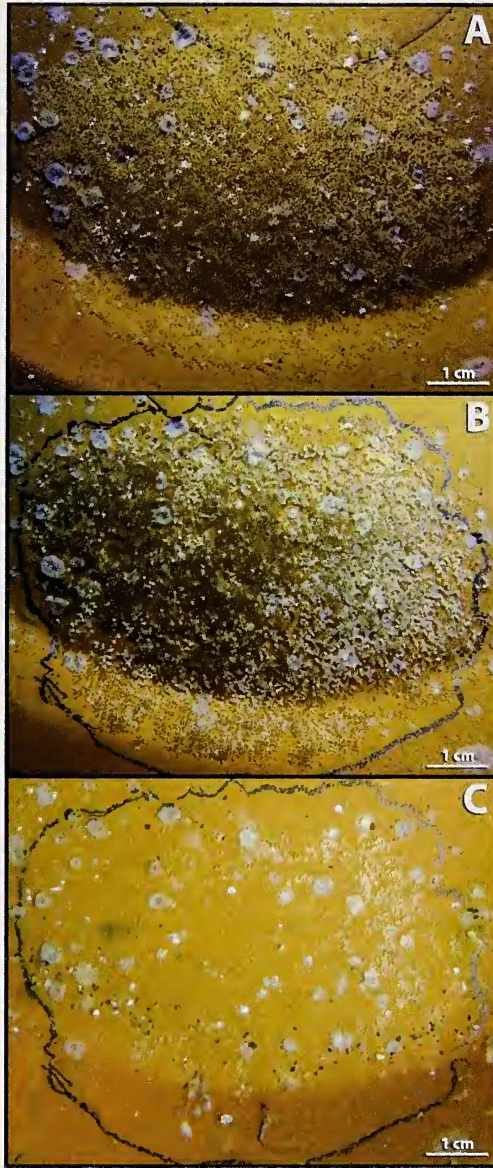
Fig. 3.   Sequential weekly photographs of a single brood of eggs in a nesting saucer. A) Eggs in the recently laid brood appear pink/orange and the density of eggs is relatively uniform. B) Changes in color are seen within 7 days and close inspection reveals developed embryos inside eggs. C) After 14 days, all surviving larvae have emerged and the nest surface is bare.

(± 4) eggs cm^{-2} (mean $\pm$ SE, $n = 240$). As described by Ebert and Turner (1962), recently laid eggs appeared pink/orange (Fig. 3A), transitioning to transparent as they developed (Fig. 3B). The eyes of developing embryos were visible in late-stage eggs, allowing differentiation of several clutches in a single nest. Identifiable individual clutches were observed in sequential photos taken a week apart on several occasions (Fig. 3), establishing a minimum incubation period of 7 days. Assuming eggs hatched within 24 hours after the second photograph of the
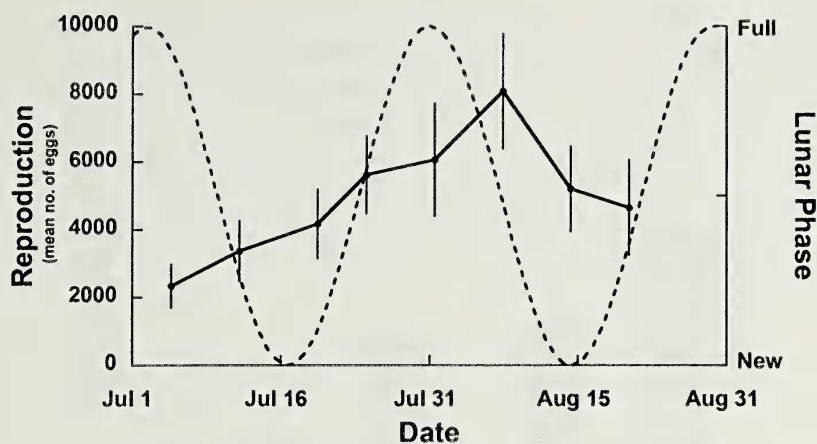
Fig. 4.   The average number of eggs produced by reef populations (solid) relative to lunar phase (dashed) during two months in 2012. Cyclical patterns, coinciding with lunar phase or tidal amplitude were not apparent (see Results). Error bars represent ± 1SE.

sequence, or 24 hours prior to the third photograph, then egg incubation time was between 8 and 13 days.

Blackeye gobies did not appear to time reproductive effort with any particular lunar phase, producing similar numbers of eggs during all four lunar phases (Pseudo-$F_{3,57} = 0.69, p = 0.56$, Fig. 4) and a similar number of nests during all four phases (27-33 nests). Moreover, reproductive output was unrelated to tidal amplitude, with similar numbers of eggs produced (mean ± SE: 4461 ± 607 vs. 5461 ± 673 eggs; Pseudo-$F_{1,19} = 1.81, p = 0.18$) and similar numbers of active nests during spring and neap-tide periods (56 and 66), respectively.

Reproductive output was negatively correlated with water temperature (Spearman rank correlation: $r = -0.89, p = 0.02$), being higher on reefs in cooler portions of the study area than in warmer areas. This relationship appeared to be non-linear, with similar high reproductive output on reefs with average temperatures below 18°C, declining on reefs with average temperatures between 18 and 19°C (Fig. 5). Deeper reefs were colder on average than shallower reefs, as were reefs closer to the mouth of the cove compared to those in the middle or near the back (depth: $F_{1,336} = 19.77, p < 0.001$; position: $F_{2,336} = 13.77, p < 0.001$; depth x position interaction: $F_{2,336} = 2.56, p < 0.08$; Fig. 6a). Reproductive output, however, did not differ statistically between depths or among positions (depth: $F_{1,14} = 2.34, p = 0.15$; position: $F_{2,14} = 0.08, p = 0.92$; depth x position: $F_{2,14} = 0.35, p = 0.71$) due to high reef-to-reef variation (Fig. 6b).

The presence of a nest with eggs on a reef did not alter the multivariate behavioral response of fish living on that reef (Egg Presence × Fish Class interaction: Pseudo-$F_{2,414} = 0.18, p = 0.99$; Egg Presence: Pseudo-$F_{1,414} = 1.06, p = 0.35$; Fig. 7). Despite the absence of a statistically significant difference in the multivariate behavioral response between times with eggs present vs. absent, males foraged 41% less when eggs were present (mean ± SE: 0.55 ± 0.08 vs. 0.94 ± 0.18 bites per 5 min.; univariate PERMANOVA: Pseudo-$F_{1,138} = 5.24, p = 0.03$). Regardless of egg presence on a reef, behavioral rates differed among fish classes (Fish Class: Pseudo-$F_{2,414} = 65.34, p = 0.001$). Males were the most aggressive, females were intermediate, and juveniles were the least aggressive (Fig. 7). Feeding rates were the opposite, with juveniles feeding the most and males the least. Males courted and nested, whereas females and juveniles did not.
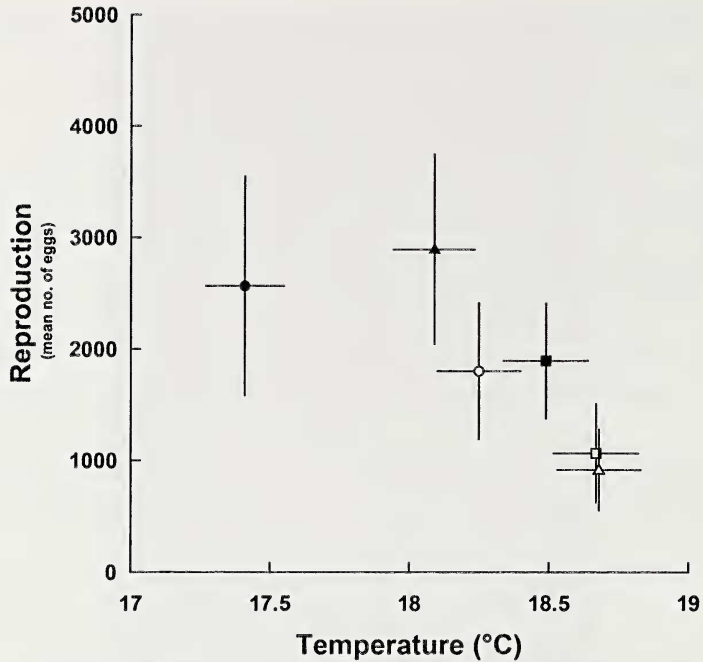
Fig. 5.   Negative relationship between blackeye goby egg production and temperature. Reef Depth: closed = deep, open = shallow. Reef position: circle = far, triangle = middle, square = near. See Results for statistical details.

Discussion

Although reproductive lunar synchrony is thought to be prevalent in tropical habitats (Johannes 1978), it is relatively uncommon in temperate waters. Blackeye gobies appear to follow that trend, as they did not exhibit any noticeable lunar or tidal cycle in their reproductive activities. Thresher (1984) noted several hypotheses that would select for lunar reproductive patterns in marine organisms, two of which could explain the lack of lunar synchrony in blackeye gobies. One hypothesis is that reproduction is timed so that larvae hatch when food densities are high, which could have a lunar pattern. The other hypothesis is that lunar phase is a convenient way to synchronize reproductive efforts among numerous individuals (including those of multiple species), reducing larval mortality by swamping their predators. Johannes (1978) noted that temperate reef residents experience lower larval predation than tropical reef residents, which might result in lower selection for lunar synchrony of reproduction in temperate species like the blackeye goby. Similarly, a lack of lunar pattern in larval food abundance could explain a lack of lunar pattern in reproduction. Instead, continuous reproduction without lunar pattern might maximize lifetime fitness.

The absence of lunar synchrony might also be attributable to the long and variable larval duration of the blackeye goby. During their roughly two-month-long pelagic phase (Block 2011), larvae would experience several lunar cycles. Thus, timing reproductive effort to a particular lunar phase may result in negligible fitness gains. The large range of size at settlement in the blackeye goby (16 to 25 mm SL; Watson 1996), coupled with a variable pelagic duration, suggests variation or flexibility in larval growth rates and settlement potential. Larvae have been known to delay metamorphosis (McCormick 1999) despite having reached adequate settlement size (Victor 1986), presumably increasing exposure to potential settlement habitat. A similar
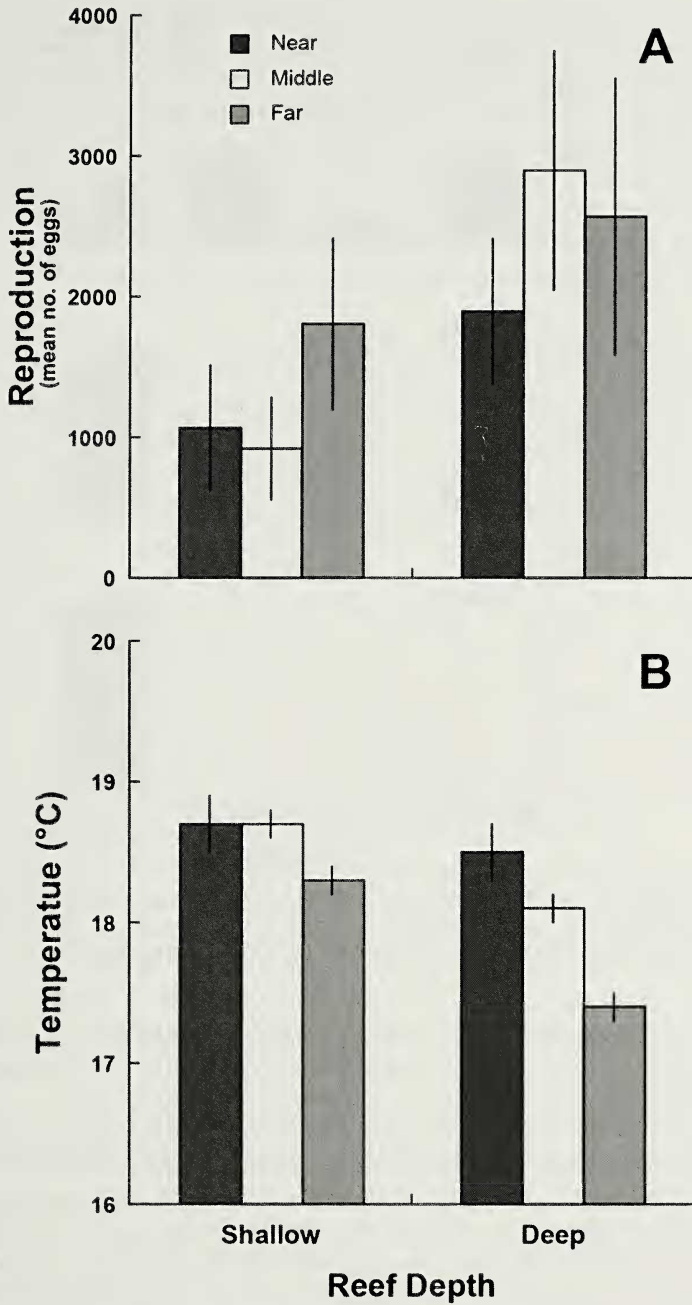
Fig. 6. A) Average egg production of blackeye gobies pooled over eight weeks for each reef depth and position combination during 2013. Differences in reproduction between depths or among positions were not statistically significant. ($n = 24$ or 32 for each group). B) Average temperature during the same eight weeks for each reef depth and position combination. Deep reefs and reefs farther from the back of the cove were colder than shallower reefs and reefs closer to the back of the cove ($n = 57$ days per bar). Error bars represent $\pm$ 1SE (see Results for statistical details).
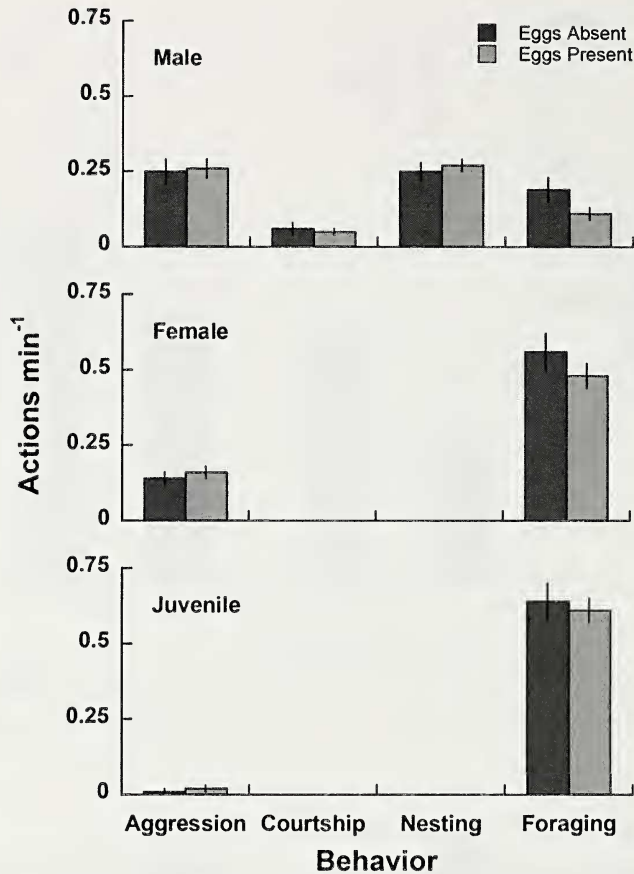
Fig. 7. Rates of behavioral expression when eggs were present in a nest on a reef or not, in the three classes of blackeye goby: male, female, and juvenile. The presence of eggs in a reef nest did not influence behaviors except male foraging (see Results). Means $\pm$ 1SE are shown ($n = 140$ observations per bar).

process may exist in blackeye gobies, promoting continuous reproduction, which supplies a pelagic larval stock that is capable of delayed and selective settlement, thus reducing risk of reproductive failure.

Temperature varied significantly within our array of reefs, and reproductive output reflected differences in temperature, decreasing with increasing temperature. Deeper reefs and reefs closer to the mouth of the cove were colder than shallower reefs and those nearer the back of the cove. These differences in temperature are due to the amount of time that those areas spent under the thermocline (MJS and MAS, *personal observations*). Differences in temperature are correlated with differences in nutrient concentrations (Dayton 1985; Dayton et al. 1998) and perhaps food availability (e.g., zooplankton). Therefore, differences in reproduction related to water temperature might not be driven by temperature differences per se. Nevertheless, temperature and day length are generally recognized as the two of the most widespread environmental cues for seasonal reproduction, and within the reproductive season, there may be thermal optima (Shrode and Gerking 1977; Gerking et al. 1979). The wide geographic range (British Columbia to Baja California) and depth range (intertidal to 80 m; Love 2011) occupied by the blackeye goby indicates that it is adapted to a wide range of temperatures, but reproduction may be reduced at warmer times or places.

We documented blackeye goby reproduction during each month from July through late March. When coupled with Ebert and Turner's (1962) account of nesting from April through October, there is documented evidence for year-round reproduction by the blackeye goby in southern California, supporting claims of year-round reproduction by Love (2011). Breitburg (1987) observed reproduction only between March and October at her study site near Santa Barbara, California. It is possible that reproduction occurs year-round in warmer locations but only seasonally in cooler areas. Temperature is known to affect both incubation time (Lasker 1964; Miranda et al. 1990) and larval growth rates (O'Connor et al. 2007) which may help explain the seasonality observed in populations experiencing cooler average annual temperature.

Our estimates of brood size were more than five times greater than the 1700 eggs in a single nest reported by Ebert and Turner (1962). Based on Wiley's (1973) estimation of female fecundity ranging from 3274 to 4788 eggs ($n = 4$ females), a minimum of two females would be necessary to account for the 8663 eggs per nest recorded in this study; however, female sizes were not included with Wiley's estimates. Since female fecundity is known to increase exponentially with body length (Duarte and Alcaraz 1989) it is possible that a single large female could produce the average number of eggs observed here. Conversely, the large number of eggs per nest found in the present study could be the product of multiple females spawning in a single nest over a short period of time. If female blackeye gobies exhibit similar nesting preferences and habits as a number of damselfishes that have been studied, multiple females may lay eggs in a single nest over a short period, producing what appears to be a single large clutch (Sikkel 1989; Knapp et al. 1995). Love (2011) stated that males may defend the clutches of up to 6 females; however, one or two females appears to be typical, which is in line with a reported population sex ratio of 1.7 females per male (Wiley 1973). Although more than one clutch in a single nest was observed on several occasions (based on the presence of non-contiguous clutches and eggs of different stages), the majority of nests appeared to contain a single clutch.

The exact incubation period for blackeye goby eggs could not be determined from our once-a-week photos, but it must have been more than 7 days and less than 14. While increasing the frequency of nest observations could provide a more accurate estimate of incubation time, the consistent disruption necessary might also result in nest abandonment or filial cannibalism by guarding males, biasing estimates low. An attempt was made to passively observe reproduction in clear acrylic aquaria equipped with flow through seawater, but no eggs were produced in either of two lab populations over a month. Aquaria were set up similar to the small reefs used in the field (i.e., rock rubble collected under water and artificial nesting saucers), but sand was not included, as it would have obscured the view of the nest.

Behaviors of males, females, and juveniles were mostly unaltered by the presence of eggs on the reef. Surprisingly, rates of aggression and nesting behavior by males did not change despite guarding a nest containing eggs. Foraging rates of males guarding eggs were, however, about 40% lower than when eggs were absent. While eggs were present in the nest, males continued to court females, despite the potential for damaging or dislodging eggs already in the nest. The costs and benefits of the behaviors we quantified may depend on context, however. For example, work on other fishes has shown that territorial defense can be affected by population density (Warner and Hoffman 1980); and male foraging rates can be influenced by male territorial strategies (Hoffman 1983). Although we stocked our artificial reefs with densities reflecting those on natural reefs at Catalina at the time ($\sim$6 individuals m^{-2}, MJS pers. obs.), higher densities are sometimes observed in nature, e.g., up to 20 individuals m^{-2} (Love 2011; Steele, unpublished data). Behavioral responses to the presence of nests with eggs might differ in those higher-density populations. More artificial nest sites were present on our reefs than were used,

indicating this resource was not limited, which could alleviate density-dependent competition for preferred nesting space.

Results from this study indicate that blackeye gobies reproduce year-round, and without any lunar or tidal patterns. These findings suggest this species maximizes reproduction over a protracted period and it employs a bet-hedging strategy by spreading out reproductive efforts, thereby reducing the risk of reproductive failure. Whether this reproductive strategy is employed by the blackeye goby throughout its very broad geographic range is an interesting question that is amenable to study because reproductive output in this species is relatively easy to measure using the methods described in this paper.

Acknowledgements

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